On the breeding of the Redpoll *Carduelis flammea* in NE Finland[1]

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PULLIAINEN, E. & V. PEIPONEN 1981: *On the breeding of the Redpoll* Carduelis flammea *in NE Finland.* — Ornis Fennica 58:109—116.

The paper is based on 332 nest records made in Itäkaira, NE Finland, in 1970—80. The favourite nesting habitats were mountain birch and fresh mixed lowland forests, and the preferred nest sites were junipers and spruces. The commencement of egg-laying and the length of the laying season varied considerably from year to year. The eggs were laid at intervals of c. one day. Complete clutches contained 2—7 eggs, the most usual number in every summer being 5. The local clutch size decreased by an average of 0.02 eggs per day during the course of the breeding season. The incubation period was 10—12 days and the nestling period 9—13 days. The breeding strategy of the species is interpreted as an adaptation to the utilization of varying seed resources.

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Introduction

When we commenced studies on the breeding biology of the Redpoll *Carduelis flammea* in 1970, our minds were occupied with Lack's (1968) idea that the characteristics of breeding in birds, such as laying date, clutch size and duration of the nestling period, have all evolved to produce the greatest possible number of surviving young. Once the data from 11 successive summers had been collected, it also seemed worth while to establish the extent to which the ideas of Wiens & Johnston (1977) on the breeding strategies of granivorous birds hold good in the case of the Redpoll, a species which can even raise its young on a pure seed diet (Witt-Strömer et al. 1956, Peiponen 1962, Järvinen & Pietiäinen 1981). The breeding of the Redpoll in northernmost Fennoscandia has been dealt with earlier by Peiponen (1967), Hildén (1969), Enemar (1969), Haftorn (1971), Pulliainen (1979a) and Järvinen & Pietiäinen (1981), among others.

The purpose of the present paper is to provide the main results of our studies on the habitat, nest site selection and breeding of the Redpoll in eastern Finnish Forest Lapland.

Material and methods

Field observations were made in the surroundings of the Värriö Subarctic Research Station

[1] Report No. 117 from the Värriö Subarctic Research Station of the University of Helsinki.

(67°44'N, 29°37'E) in the summers of 1970—80. Members of the station staff carried out systematic daily surveys, each in his own study plot, in an area comprising pure spruce *(Picea abies;* 26.5 %) and pure pine *(Pinus sylvestris;* 18.5 %) forests, and mixed forests (22.0 %) of spruce, pine and birch *(Betula* spp.), as well as bogs (13.5 %), lowland birch forests (3.0 %), subalpine birch forests (7.0 %) and alpine fell summits (9.5 %). In all 332 nests were found, but some of them yielded very few data. For this reason, no data on nesting success are presented.

Results

Nesting habitats and nest sites. The nesting habitats of 303 Redpoll pairs in the study area were:

	No. of pairs	%
Mountain birch forest	120	39.6
Fresh mixed lowland forest	71	23.4
Birch-juniper forest	23	7.6
Juniper scrub	18	5.9
Spruce bog	16	5.3
Spruce forest by brook	16	5.3
Pine forest on dry heath	14	4.6
Birch forest by brook	10	3.3
Pine peat-bog	9	3.0
Almost treeless fell summit	3	1.0
Birch-pine forest on dry heath	3	1.0

In 1970, 1971, 1973, 1974 and 1976 at least half the nests found were in mountain birch forests, and in 1979 49 of the 100 nests were in fresh mixed lowland forests.

Of 310 nests, 175 (56.5 %) were in junipers, 78 (25.2 %) in spruces, 43 (13.9 %) in birches, 11 (3.5 %) in pines, 2 (0.6 %) on stumps and 1 (0.3 %) in a willow bush *(Salix caprea).*

The heights of the nests above the ground in the junipers, spruces, birches and pines are shown in Fig. 1. The corresponding mean heights ($\pm SD$) were 0.7 ± 0.2, 4.3 ± 3.0, 2.7 ± 1.7 and 3.6 ± 3.3 m. Of 71 nests, 44 were adjacent to the main trunk, 13 at a distance of 1—50 cm from it, 7 at 51—100 cm and 7 over 100 cm. All the nests in birches and 3 of the 4 in pines were adjacent to the main trunk, probably owing to the structure of the trees in question. The majority of the 80 nests examined were on the south side of the trees:

N	NE	E	SE	S	SW	W	NW
11	8	12	17	17	10	4	1

Of the 224 Redpoll nests studied by Hildén (1969) at Karigasniemi (69° 30'N), 52.2 % were in junipers, which corresponds well with our results, while at Kilpisjärvi (69°N) the bulk of the nests were located in birches (Peiponen 1967). In southern and central Finland, on the other hand, spruces (50—77 %) appear to be the favourite nest site of the Redpoll (Peiponen 1967, Hildén 1969, Antikainen et al. 1980; see also Leino 1973). In our study area the nests located in the upper halves of the tall Lappish spruces could be found only by following the activities of the Redpoll parents. It is thus possible that the real proportion of spruces among the nest sites was greater than recorded here.

Dense, bushy junipers, especially common in mountain birch and certain lowland birch forests, evidently offer good shelter for the Redpoll nest. In pines and especially in spruces the nests are mainly on the SW, S, SE and E sides, where in Lapland the branches are generally longer and leafier. The thrush *Turdus* spp. and the Pine Grosbeak *Pinicola enucleator* also build their nests mostly on these sides of conifer trees (Pulliainen 1978, 1979b).

Egg-laying and clutch size. The commencement of egg-laying and the length of the laying season varied considerably from year to year (Fig. 2). In two of the 11 summers egg-

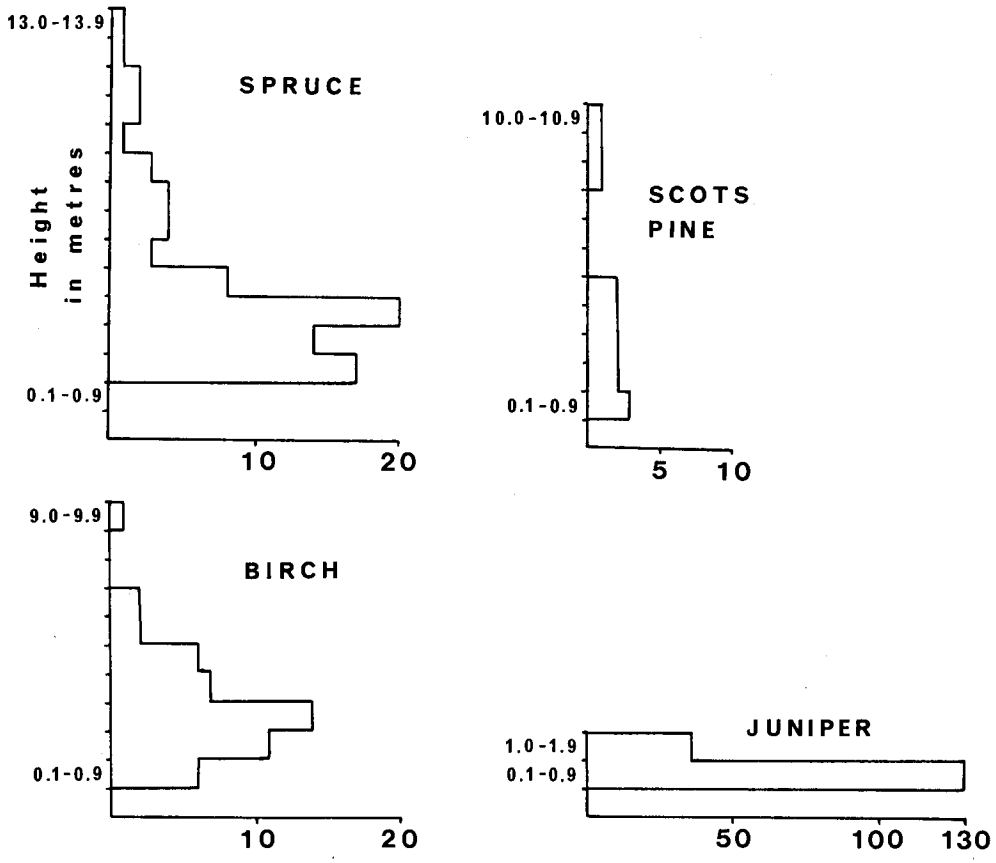

FIG. 1. Heights above the ground of nests of the Redpoll in spruces, pines, junipers and birches in NE Finland.

laying started before 22 May and in three cases only after 10 June. Clear peaks occurred the period 22—31 May in 1979, on 1—10 June in 1970 and 1974, and on 11—20 June in 1971. The latest clutches were started at the end of July (in 1970). The length of the egg-laying season varied from a few days to about two months. The median date for the first egg varied less, but still considerably, viz. between 28 May and 19 June (Table 1).

The present Redpolls usually laid their eggs at intervals of about one day, like small passerines in general, but in one case 6 eggs were laid in 5 days and in one case 6 eggs in 4 days.

In each of the summers in which substantial numbers of clutches were recorded the most common size for a completed clutch was 5 eggs (Table 2). The size ranged from 2 to 7, averaging 5.0 ± 0.8 ($N = 94$; Table 2).

The equation of the linear regression of clutch size (y) on the number of the day (x; 20 May = 1, etc.) is

$y = 5.360 - 0.017x$ ($r = -0.300$)

and the parabolic regression equation

$y = 5.101 + 0.011x - 0.0005x^2$.

The laying date explains 9 % of the

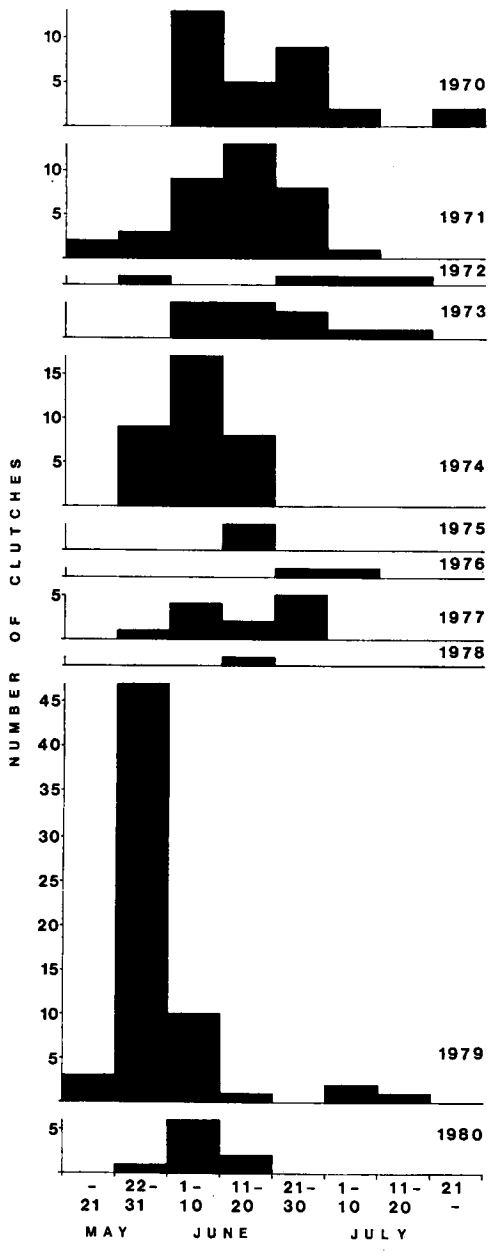

FIG. 2. Commencement of egg-laying by the Redpoll in NE Finland in 1970—80.

variation in clutch size according to the former equation and 11 % according to the latter. Thus the linear decrease of clutch size averages 0.02 eggs/day.

Incubation. Only the female was seen incubating, and she was fed at the nest by her mate, as reported by several earlier researchers (see also Pulliainen 1979a). The lengths of 20 incubation periods were 10 (7 cases), 11 (12) and 12 (1) days, the mean being 10.7 days.

Hatching and nestling period. In 12 of 16 cases hatching was completed within less than 2 days. Of 103 eggs incubated for the full period, 92.3 % hatched, the hatching success varying between 86.5 % and 100.0 % in different summers. These are high percentages compared with those reported by Hildén (1969) and Enemar (1969) from Finnish and Swedish Lapland — 76.7 and 75.5 %, respectively.

The length of the nestling period varied as follows: 2x9, 1x10, 3x11, 4x12 and 4x13 days, the mean being 11.5 days.

Discussion

The Redpoll is a characteristic inhabitant of the northern taiga and adjacent subarctic birch zone, but is very capricious in its occurrence. It may overwinter in the area (even roosting and feeding in the snow; Cade 1953, Sulkava 1969) if enough birch seed is available, but the numbers of the overwintering individuals vary markedly from year to year (see also Järvinen & Pietiäinen 1981). During the present period of 11 successive summers there was at least one nest

record per summer, but in more southerly areas the species may be absent for years, only to reappear in great numbers when a good supply of acceptable food is available (e.g. Peiponen 1957, 1967, Hildén 1969, Leino 1973, Antikainen et al. 1980).

The Redpoll accepts a wide variety of seeds; besides those of *Alnus, Larix, Filipendula, Epilobium, Polygonum, Matricaria* and *Myrtillus* it includes seeds of *Betula* spp. and *Picea abies* (e.g. Peiponen 1957, 1962, Svärdson 1957, Evans et al. 1967, Evans 1969, Hildén 1969, Leino 1973, Antikainen et al. 1980, Järvinen & Pietiäinen 1981). The two latter types of seeds are the main components of the diet, but during the summer months animal matter may sometimes compose 80 % of the food of adults and 90 % of that of the young (Peiponen 1962). The seed yields of birches (Sarvas 1949) and the quantity and quality of the spruce seed crop (Sarvas 1957, Pulliainen 1973, 1974) vary markedly from year to year, especially in the northern taiga. In the best cases, the Redpolls have sufficient supplies of good-quality food for nesting from the beginning of the dehiscence of spruce seed in March until August, when the abundance of insects and other invertebrates decreases drastically.

TABLE 1. Laying seasons and nesting medians of the Redpoll in NE Finland in 1970—80. The start of the laying season was taken as the date when the first egg was laid.

Year	Laying season	Nesting median	No. of clutches
1970	8 June — 27 July	16 June	26
1971	19 May — 25 June	8 June	20
1972	(28 June)	—	1
1973	8 June — 13 July	19 June	9
1974	25 May — 16 June	6 June	20
1975	(12—13 June)	—	2
1976	(26 June)	—	1
1977	29 May — 29 June	13 June	13
1978	(13 June)	—	1
1979	20 May — 18 July	28 May	43
1980	29 May — 19 June	7 June	9

Redpolls are known to have used the whole of this potential breeding season from March (Witt-Strömer et al. 1956) to August (Salkio 1952). In the present study area, however, the length of the egg-laying season varied from only a few days to about 2 months. The intensity of the search for Redpoll nests in different habitats did not vary significantly from summer to summer, but in 5 of the 11

TABLE 2. Clutch size of the Redpoll in Itäkaira, NE Finland, in 1970—80.

Clutch size	Number of clutches										
	1970	1971	1972	1973	1974	1975	1976	1977	1979	1980	Total
2	—	—	1	—	—	—	—	—	—	—	1
3	—	—	—	—	—	—	—	—	1	—	1
4	5	—	—	1	1	1	1	—	6	—	15
5	11	2	—	5	8	1	1	4	20	6	58
6	1	2	—	1	5	—	—	2	3	3	17
7	—	—	—	—	2	—	—	—	—	—	2
Mean	4.8	5.5	2.0	5.0	5.5	4.5	4.5	5.3	4.8	5.3	5.0
± *SD*	0.6	0.6		0.6	0.8	0.7	0.7	0.5	0.6	0.5	0.8
N	17	4	1	7	16	2	2	6	30	9	94

summers at least half the nests were found in mountain birch forests and in one summer 49 % occurred in fresh mixed lowland forests. During the other summers they were more evenly distributed among the available habitats. The parents were seen to pick up seed of *Betula* spp., *Picea abies* and *Vaccinium myrtillus,* and insects (checked from the crop contents of nestlings). No exact data are available, but the supplies of the acceptable foods probably affected the choice of nesting habitat and nest site, for deciduous trees and bushes, and junipers chiefly occur in mountain birch forest. Redpoll nests are usually well hidden in trees or bushes.

Initiation of breeding activity by the Redpoll cannot be associated with photoperiodic changes, but is probably nearer the pattern of the Quelea *(Quelea quelea)* in sub-Sahara Africa. Jones & Ward (1976) suggest that breeding colonies of the Red-billed Quelea can form only when sufficient protein-rich food is available for the females to accumulate the reserves necessary to initiate egg production and sustain the rapid decline in body protein during egg formation. Seeds can be the sole source of protein for the Redpoll (see also Brooks 1968), and the crude protein content (as % of dry matter) of spruce seed in the northern Finnish taiga is known to vary at least within the range 10—22 % (crude fat content 7—32 %) (Pulliainen 1973). Insect matter is naturally rich in protein.

Populations with high reproduction and rapid turnover may be able to respond readily to environmental changes and exploit new resources (e.g. good tree seed yields) by changes in their numbers (Holling 1965). Efficient exploitation of seed crops may be facilitated by a short breeding cycle (Wiens & Johnston 1977). The breeding cycle of the Redpoll is in fact rapid; in the present study incubation lasted only 10—12 days and the nestling stage 9—13 days, and these periods accord with earlier records (Grinnell 1943, Baldwin & Reed 1955, Peiponen 1962, Hildén 1969, Pulliainen 1979a). The factors responsible for this breeding pattern include the following: (a) the female leaves her nest unattended for only 3.4—5.0 % of the incubation period (Peiponen 1962, 1970, Pulliainen 1979a), (b) the incubating and brooding female is almost wholly dependent on her mate for nutrition (Pulliainen 1979a), (c) the young are fed only 45 times/day, on average, but on each occasion receive large portions from the feeder's crop (Peiponen 1970, Pulliainen 1979a), and (d) the seed-insect food mixture is probably optimal for growing nestlings (Pulliainen 1979a). This rapid breeding cycle also reduces competition with other sympatric resident species, minimizing the duration of territorial overlap (see also Rowley & Vestjens 1973).

High reproduction may also be obtained by a large clutch (Lack 1968; see also Drent & Daan 1980). In our material, however, the mean clutch size of the Redpoll was only 5.0. Laying of additional eggs would lengthen the breeding cycle without improving the breeding result. Murray (1979) speculates that the clutch represents the fewest eggs that a female with given probabilities of survival can produce during each reproductive effort and still be able to replace herself and her mate in the next generation. The Redpoll seems to ensure breeding success by multiple broods either in the same area (Troy & Shields 1979), if the food supply allows, or in different areas (e.g. Peiponen 1967, Hildén 1969).

Acknowledgements. The authors wish to thank the staff of the Värriö Subarctic Research Station and also Mr. Timo Lumme and Mr. Esko Rajala for technical assistance. They are grateful to the National Research Council for the Natural Sciences (Valtion luonnontieteellinen toimikunta) for financial support, and to Dr Peter Evans, Dr Olavi Hildén and an unknown referee for fruitful criticism concerning an earlier draft of this manuscript.

Selostus: Urpiaisen pesimäbiologiasta Koillis-Suomessa

Urpiaisen pesimäbiologiaa on tutkittu Itäkairan itäosassa (67°44'N, 29°37'E) vuosina 1970—80, jolloin löydettiin yhteensä 332 pesää. Urpiaisille oli tarjolla pesimispaikoiksi kuusi-, mänty-, koivu- ja sekametsiä sekä erilaisia soita ja tunturipaljakoita. Ne suosivat tunturikoivikoita ja alempana sijaitsevia tuoreita sekametsiä, joista löytyi 63 % pesistä. 56.5 % pesistä sijaitsi katajissa ja 25.2 % kuusissa. Kuva 1 osoittaa pesien etäisyyden maanpinnasta katajissa, kuusissa, koivuissa ja männyissä. Pesät sijaitsivat useimmiten oksan päällä rungon vieressä sen eteläpuolella, missä Lapin havupuiden oksat ovat pitemmät ja tuuheammat kuin pohjoispuolella.

Muninnan alkamisajankohta ja munintakauden pituus vaihtelivat 11 kesän aikana merkittävästi vuodesta toiseen (kuva 2). Kahtena kesänä munintа alkoi ennen toukokuun 22 päivää. Vuonna 1970 munintaa tapahtui vielä heinäkuun lopulla. Muninnan alun mediaani vaihteli vähemmän, mutta kuitenkin huomattavasti, rajoissa 28.5.—19.6. (taul. 1).

Muniminen tapahtui keskimäärin päivän välein. Munaluku vaihteli rajoissa 2—7, keskiarvo 5.0 ja yleisin munaluku niinikään 5. Tutkimusalueella näiden kesien aikana munaluku laski lineaarisesti keskimäärin 0.02 munaa vuorokaudessa, muninta-ajankohdan selittäessä 9 % munaluvun vaihtelusta.

Haudonta kesti 10—12 (keskiarvo 10.7) ja pesäpoikasaika 9—13 vrk (keskiarvo 11.5). 92.3 % munista kuoriutui. Kahdessatoista 16:sta tapauksesta pesyeen munat kuoriutuivat alle kahden vuorokauden kuluessa. Vain naaras hautoo koiraan ruokkiessa sitä pesällä.

Urpiaisen munamäärän sekä lyhyen haudonta- ja pesäpoikasajan todetaan olevan sopeutumia määrältään ja laadultaan vaihtelevien siemensatojen hyväksikäyttämiseen nomadisten vaeltelujen aikana. Kilpailu sympatristen lajien kanssa jää näin lyhytaikaiseksi.

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Received April 1981, revised September 1981